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RESOLVING PHYLOGENETIC AND TAXONOMIC CONFLICT IN *BEGONIA*

Begonia Phylogeny Group
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Begonia is the world's fastest-growing genus and a focus of intense taxonomic research. To support this, a stable and useful sectional classification is needed. This paper reviews the feasibility and challenges of creating an infrageneric classification for *Begonia* based on phylogenetic data, and how to overcome phylogenetic and taxonomic conflict. In particular, it (i) tests genus-wide patterns of incongruence between phylogenies based on the nuclear, chloroplast and mitochondrial genomes; (ii) explains organelle inheritance and its contribution to phylogenetic incongruence, and (iii) presents a manifesto for a workable and stable subgeneric classification in light of the above and lays the foundation for a collaborative Begonia Phylogeny Group.

Keywords. Classification, taxonomy.
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Introduction

Taxonomy is the cornerstone of biology and is essential for understanding and conserving biodiversity (Mace, 2004). The ability to define allied groups of species facilitates species identification and description and supports investigations into areas such as biogeography and the evolution of morphology and traits. In many plant families, such groups are

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circumscribed as genera; Humphreys & Linder (2009) note that 'good' genera are stable and predictive, and that useful genera are diagnosable and of a workable size.

In the megadiverse family Begoniaceae C.Agardh., the role of the genus is largely fulfilled by the infrageneric rank of section within the genus *Begonia* L. The 2089 species currently accepted in *Begonia* are divided among 70 sections, which would ideally have the qualities listed by Humphreys and Linder (see *Discussion*).

The rate at which new species are being added to *Begonia* remains high; more than 200 have been published since the synopsis of the genus produced by Moonlight *et al.* (2018). Species from this current flood of discovery need stable, predictive and diagnosable taxonomic homes of a workable size. These qualities are not found in all sections of the genus, no matter which classification is followed.

The first modern synoptic species-level classification of the sections of *Begonia*, by Doorenbos *et al.* (1998), covered c.1400 species divided between 61 sections and laid the foundation for future work on the genus. The authors did not erect any new sections, but their classification is widely acknowledged as a sound review of species morphology on which to base useful and insightful notes on sectional delimitation. Since the classification by Doorenbos and colleagues, and before any further genus-wide synopsis, three new sections were published: *Begonia* sect. *Chasmophila* J.J.de Wilde & Plana, *Begonia* sect. *Oligandrae* M.Hughes & W.N.Takeuchi, and *Begonia* sect. *Microtuberosa* Moonlight & Tebbitt, the last of which is supported by the results of molecular phylogenetic analysis (Moonlight *et al*., 2017).

The first DNA-informed classification to cover the whole genus (Moonlight *et al*., 2018) was based on three non-coding chloroplast regions (*ndh*A, *ndh*F–*rpl*32, *rpl*32–*trn*L), and a taxon sampling of 574 species. The authors were relatively conservative regarding deviations from previous classifications, making sectional recircumscriptions only when such changes were sufficiently supported by taxon sampling. Five sections were synonymised, four sections were reinstated, and five new sections were raised. With the addition of the new sections (*Begonia* sect. *Astrothrix* Moonlight, *Begonia* sect. *Ephemera*

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Moonlight, *Begonia* sect. *Jackia* M.Hughes, *Begonia* sect. *Kollmannia* Moonlight, and *Begonia* sect. *Stellandrae* Moonlight), a total of 70 sections were recognised.

Since publication of the classification by Moonlight *et al.* (2018), two further changes have been made to sectional delimitation. One new section, *Begonia* sect. *Flocciferae* N.Krishna & Pradeep, has been raised, and another section, *Begonia* sect. *Semibegoniella* (C.DC.) F.A.Barkley & Baranov, has been sunk into synonymy with *Begonia* sect. *Casparya* (Klotzsch) Warb. based on molecular phylogenetic evidence (Jara-Muñoz *et al.*, 2019).

The most recent whole-genus classification (Shui *et al.*, 2019) was based on full chloroplast genomes but with a taxon sampling of only 98 species, representing 29 of the 70 sections in Moonlight *et al.* (2018). Based on a phylogeny largely congruent with Moonlight *et al.* (2018) but with 17% of the taxon sampling, the infrageneric taxonomy of *Begonia* was completely reorganised, based on a strict monophyly criterion, into 14 subgenera and 48 sections.

The preference for monophyly at all costs resulted in a sectional taxonomy of limited utility and left some sections without any usable diagnostic characters. A major shortcoming of the Shui *et al.* (2019) classification is the subsuming of the vast bulk of species across Southeast Asia into a grossly enlarged section *Petermannia* (Klotzsch) A.DC. containing 617 species lacking any diagnostic characters and covering a huge range of growth forms and vegetative and reproductive character diversity. This leaves taxonomists working in countries with the highest *Begonia* species diversity without a sectional classification.

A similar level of taxonomic lumping was also found in *Begonia* sect. *Begonia*, which according to Shui *et al.* (2019) contains species previously placed in *Begonia* sect. *Casparya*, *Begonia* sect. *Solananthera* A.DC. and *Begonia* sect. *Diploclinium* (Lindl.) A.DC. However, this expanded section is diagnosed as consisting of non-tuberous perennials, even though its circumscription contains both tuberous species and around half of the short-lived annuals in the Americas. Hence, we now have two contrasting classifications based on the chloroplast

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genome. However, there is also further complexity because phylogenetic incongruence between organelle genomes is well supported (Goodall-Copestake *et al.*, 2010; Fuller, 2014), and therefore the chloroplast genome is not likely to reflect the species phylogeny, regardless of how much of it is sampled.

Before any major changes are made to the sectional classification of *Begonia*, phylogenetic incongruence needs to be better understood. To address this, we constructed phylogenies representing all major clades of the genus from all organelle and nuclear genomes, using a combination of legacy data and new DNA sequence data obtained by means of both Sanger and high-throughput approaches. To test organelle inheritance, we carried out interspecies greenhouse crossing experiments within *Begonia* sect. *Gireoudia* (Klotzsch) A.DC.

In this paper, we review the feasibility and challenges of creating a subgeneric classification for *Begonia* based on a molecular phylogenetic approach, and ways in which to overcome phylogenetic and taxonomic conflict. In so doing, we:

- test genus-wide patterns of incongruence between phylogenies based on the nuclear, chloroplast and mitochondrial genomes
- explain organelle inheritance and its contribution to phylogenetic incongruence
- present a manifesto for a future workable and stable subgeneric classification in *Begonia*.

Methods

Chloroplast and mitochondrial phylogenetics

DNA sequence alignments with matching taxon sampling from all major clades of *Begonia* were built for regions of the mitochondrial and chloroplast genomes, using a combination of legacy data (Goodall-Copestake *et al.*, 2010; Thomas *et al.*, 2011; Fuller, 2014), newly generated Sanger-based sequences, and sequences assembled from high-throughput

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genome skims (Supplementary file 1 lists the accessions from which these sequences were obtained). The mitochondrial data consist of the *mat*R gene, *nad*1 intron and gene, *nad*7 introns and gene, and *rps*14–*cob* spacer, with Sanger-derived sequences using the protocol in Goodall-Copestake *et al.* (2010).

For selected species newly sampled in the present study, the same regions were assembled from 150 bp paired-end Illumina genome skims, using the Sanger-derived sequences from *Begonia laruei* M.Hughes as a reference. The assemblies were carried out in Geneious Prime 2021.1.1 (Kearse *et al.*, 2012) on trimmed reads, using the Geneious mapper with low sensitivity and iterated 2 times. Assemblies were checked visually for quality.

The chloroplast data consisted of the *ndh*A intron, the *ndh*F–*rpl*32 spacer and the *rpl*32–*trn*L spacer, the Sanger-derived content having been obtained using the protocol described by Thomas *et al.* (2011). For additional species, the same regions were assembled from 150 bp paired-end Illumina genome skims, using the Sanger-derived sequences from *Begonia bipinnatifida* J.J.Sm. as a reference (Wilson, 2021). Raw reads were trimmed using Trimmomatic-0.36 (Bolger *et al.*, 2014) and then mapped using Bowtie2 (Langmead & Salzberg, 2012), and a consensus was called using Ococo 0.1.2.7 (Brinda *et al.*, 2018), with assemblies checked visually for quality.

The chloroplast alignment consisted of 4586 sites, of which 771 were parsimony informative, and the mitochondrial alignment consisted of 6554 sites, of which 252 were parsimony informative. The data were partitioned for analysis using PartitionFinder2 (Lanfear *et al.*, 2017) on the CIPRES Science Gateway (Miller *et al.*, 2010). The chloroplast alignment and partition data are avaiiable as Supplementary files 2 and 3, respectively, and the mitochondrial alignment and partition data as Supplementary files 4 and 5, respectively).

Maximum likelihood phylogenetic analysis was carried out on both datasets using IQ-TREE 1.6.12 (Trifinopoulos *et al.*, 2016) with automatic model selection (Kalyaanamoorthy *et al.*, 2017) for each partition and ultrafast bootstrap (Hoang *et al.*, 2018) with 1000 replicates (chloroplast likelihood phylogeny, Supplementary file 6; mitochondrial likelihood phylogeny, Supplementary file 7). Bayesian phylogenetic analysis was carried out on the partitioned datasets using MrBayes 3.2.7a (Ronquist *et al.*, 2012) on the CIPRES Science Gateway, with 10,000,000 generations, sampling every 1000, and the first 25% of trees discarded as burn-in (chloroplast nexus file and Bayesian phylogeny, Supplementary files 8 and 9; mitochondrial nexus file and Bayesian phylogeny, Supplementary files 10 and 11). Trees were rooted using *Hillebrandia sandwicensis* Oliv.

Nuclear phylogenetics

It was not possible to match the legacy taxon sampling of the chloroplast and mitochondrial phylogenies exactly in the nuclear dataset; however, sampling was designed to cover the same main clades and some key species. DNA was extracted from either fresh or silica-dried samples, using a Qiagen DNEasy kit (Qiagen, Venlo, Netherlands). Approximately 1 µg

of DNA was sheared using Bioruptor Pico (Cosmo Bio, Tokyo, Japan), and the length of the sheared DNA was confirmed by electrophoresis to be about 400 bp.

Dual-indexed libraries were made for each sample, using NEBNext Ultra II DNA Library Prep kit (New England BioLabs, MA, USA), following the 400- to 500 bp insert size protocol. Groups of eight libraries were pooled into a 2 µg pool for carrying out in-solution hybridisation capture of target DNA using biotinylated RNA baits from a custom myBaits kit (MYcroarray, Ann Arbor, MI, USA).

We designed two versions of a bespoke *Begonia* bait set (Michel *et al.*, 2022); the second version differed by 96 genes that were replaced after they performed poorly at sequence capture in early experiments. The phylogeny was constructed using data assembled to genes common to both versions of the bait set. The pool of *Begonia* sect. *Coelocentrum* Irmsch. samples was captured by the first version, and the others were captured by the second. The hybridisation procedure was carried out at 65°C for 19 h, following the myBaits v2.3.2 protocol (MYcroarray).

The post-capture library pools were amplified using primers of IS5_reamp.P5 and IS6_reamp.P7 (Meyer & Kircher, 2010). Subsequently, the libraries were further quantified using a QubitTM 3.0 Fluorometer (Thermo Scientific, MA, USA), and size distribution was assessed on a Bioanalyzer (Agilent, CA, USA).

The *Begonia* sect. *Coelocentrum* samples were sequenced using HiSeq, 250 bp paired-end reads, at High Throughput Genomics Core at the Biodiversity Research Centre, Academia Sinica, Taiwan. The equimolar libraries of the non-*Coelocentrum* remaining pools were pooled together and sequenced using HiSeq, 150 bp paired-end reads.

Reads were assembled to the bait sequences using the pipeline from Nicholls *et al.* (2015). This uses a very conservative assembly method to minimise the mapping of paralogues, and a conservative consensus method that removes ambiguous sites due to allele variants. This is the same pipeline as the 'basic' one described by Michel *et al.* (2022). The concatenated alignment of 1235 genes contained 234,578 parsimony-informative characters, and 75% of the bases were constant. The alignment was 2,065,391 bases long, and 24.3% of data were missing, including N calls due to the conservative assembly method.

A phylogeny was constructed using the maximum likelihood method, treating the alignment as a single partition using IQ-TREE, with auto model selection and 1000 ultrafast bootstrap replicates. Trees were rooted using *Hillebrandia sandwicensis*. Supplementary file 12 lists the accessions from which the sequences were obtained. Supplementary file 13 shows the alignment data, and Supplementary file 14 contains the likelihood phylogeny.

Organelle inheritance

To aid our understanding of organelle inheritance, controlled crosses were set up in the glasshouses at the Royal Botanic Garden Edinburgh (RBGE), with an emasculated

Begonia heracleifolia Schltdl. & Cham. plant (RBGE accession no. 20100400) as the ovule parent in isolation from other *Begonia* individuals, and with *B. carolineifolia* Regel (RBGE accession no. 20042077) and *B. conchifolia* A.Dietr. (RBGE accession no. 20042082) as the pollen parents; all three species belong to *Begonia* sect. *Gireoudia* and share the same chromosome number (*n* = 14) (Campos-Domínguez *et al.*, 2022).

Pollen was transferred by brushing the anthers of the male flowers of the paternal parents onto the stigmas of the female flowers of the *Begonia heracleifolia* plant. Seeds from the cross were germinated, and DNA was extracted from the seedlings by using Qiagen DNeasy kits. For the cross with *Begonia conchifolia*, DNA was extracted from 47 seedlings individually. For the cross with *B. carolineifolia*, it was extracted from 16 seedlings individually and from 155 seedlings in 31 pools of five to maximise the number of individuals screened.

After screening DNA sequence alignments for suitable polymorphisms with which to distinguish the parents (Drinkwater, 2014), we used PCR–restriction fragment length polymorphism to screen for organelle haplotypes. To investigate chloroplast inheritance, PCR products of the *ndh*A intron were digested with DdeI (*Begonia conchifolia* as the pollen parent); for mitochondrial inheritance, PCR products of the *rps*14–*cob* spacer were digested with AflII (*B. conchifolia* as the pollen parent) or PCR products of the *Mat*R gene with EarI (*B. carolineifolia* as the pollen parent). The resulting digests were visualised on 2% agarose gels run at 70 V for approximately 1 h, alongside samples of the pollen and ovule parents as controls.

Results

Chloroplast and mitochondrial phylogenetics

The chloroplast gene phylogeny is congruent with the results of the analyses carried out by Goodall-Copestake *et al.* (2010) and Moonlight *et al.* (2018), also based on chloroplast data, in recovering a grade of African and Madagascan species, with two Neotropical clades and one Asian clade nested within it (**Figure 1**). Seasonally dry–adapted *Begonia* are in two clades, each sister to a Neotropical clade. The mitochondrial phylogeny is congruent with that described by Goodall-Copestake *et al.* (2010) in recovering a single Neotropical clade and an Asian clade, both nested within a grade of African and Madagascan species. Seasonally dry–adapted *Begonia* are in a grade with a single Neotropical clade nested within it. Thus, the phylogenies from the two organelle genomes are markedly incongruent when considering the relationships of the major clades, and the incongruence is well supported.

There is further-supported incongruence within the major clades, for example five species sampled from *Begonia* sect. *Petermannia* (*B. amphioxus* Sands, *B. dimorpha* S.Julia, *B. fuscisetosa* Sands, *B. laruei* and *B. malachosticta* Sands) are monophyletic in

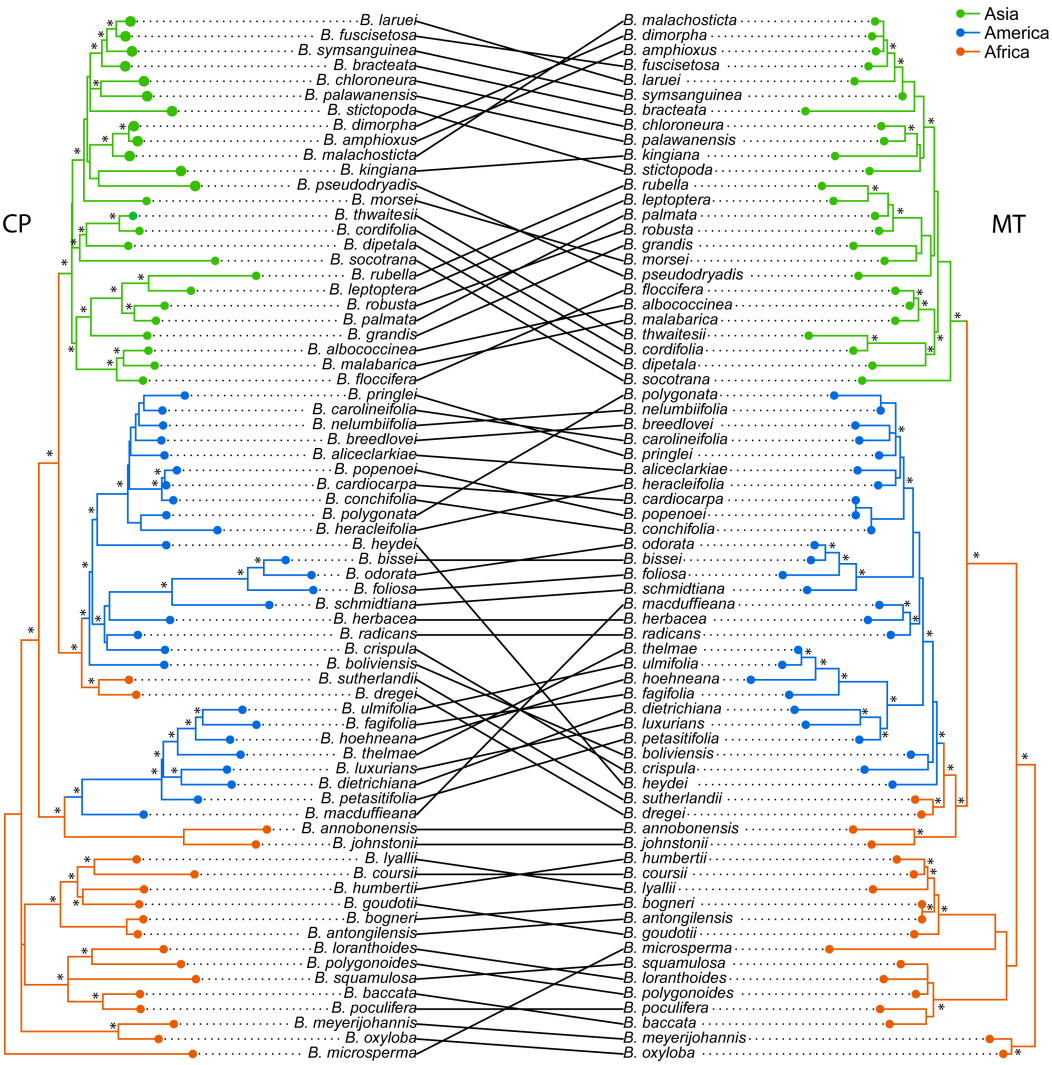

Figure 1. Maximum likelihood phylogenies of *Begonia* based on chloroplast (CP) data (the *ndh*A intron, *ndh*F–*rpl*32 spacer and *rpl*32–*trn*L spacer; left) and mitochondrial (MT) data (the *mat*R gene, *nad*1 intron and gene, *nad*7 introns and gene, and *rps*14–*cob* spacer; right). Asterisks represent fast bootstrap support of >90%. Tanglegram produced using the R package Phytools (Revell, 2012).

the mitochondrial tree but are split between two clades in the chloroplast tree. The two Neotropical clades in the chloroplast tree are not maintained within the single Neotropical clade in the mitochondrial tree, the positions of *Begonia heydei* C.DC. and *B. macduffieana* L.B.Sm. & B.G.Schub., among others, being markedly different.

Nuclear phylogenetics

The nuclear phylogeny (**Figure 2**) is based on taxon sampling different from that used to construct the chloroplast and mitochondrial trees, but the representatives of the main clades clearly show a topology more congruent with that of the mitochondrial phylogeny in that there is a single clade of Neotropical species. However, *Begonia johnstonii* Oliv. ex Hook.f. branches earlier in the nuclear phylogeny and is sister to a clade containing *B. dregei* (Otto & A.Dietr.) Klotzsch and all Asian and Neotropical species.

Organelle inheritance

The inheritance of chloroplasts and mitochondria was observed to be 100% maternal. Maternal inheritance was demonstrated for the chloroplast in the F_1 progeny of *Begonia carolineifolia* × *B. heracleifolia*, and for the mitochondria in the F_1 progeny of *B. conchifolia* × *B. heracleifolia* and *B. carolineifolia* × *B. heracleifolia*.

Discussion

Incongruence: patterns and causes

There are two possibilities for the occurrence of two lineages of chloroplasts of African origin in the Neotropics and only one apparent mitochondrial and nuclear lineage. The first is colonisation by a single individual from Africa that was heteroplasmic for chloroplasts; the second is the occurrence of two separate colonisation events from Africa, followed by subsequent hybridisation of the two lineages resulting in chloroplast capture in the genetic background of the first lineage. Either of these scenarios requires the decoupling of maternal organelle inheritance to produce the incongruence between the chloroplast and mitochondrial genomes; the first also still requires a hybridisation event in Africa to produce the heteroplasmic individual before it dispersed over the Atlantic.

The second scenario we consider to be the most likely. In a dated chloroplast phylogeny, the two Neotropical clades arrive c.10–17.5 Mya, with a considerable overlap in dates for each clade (Moonlight *et al.*, 2015, 2018). However, the lineage with only the chloroplast genotype surviving is likely to have been the second arrival, because it would have been subject to hybridisation with an established *Begonia* flora. This means that the first chloroplast lineage to arrive was probably Neotropical clade 2 (sister to the *Begonia sutherlandii* Hook.f. clade), which is widespread across the Neotropics. The second lineage to arrive was Neotropical clade 1 (sister to the *Begonia johnstonii* clade), mostly restricted to eastern Brazil, with one dispersal within South America resulting in a small clade in the northern Andes (Moonlight *et al.*, 2015).

In addition to our greenhouse experiments, the incongruent and anomalous position of *Begonia palawanensis* Merr. (*Begonia* sect. *Petermannia*) as sister to a species from *Begonia* sect. *Baryandra* A.DC. in trees based on both organelles (see **Figure 1**) is further evidence

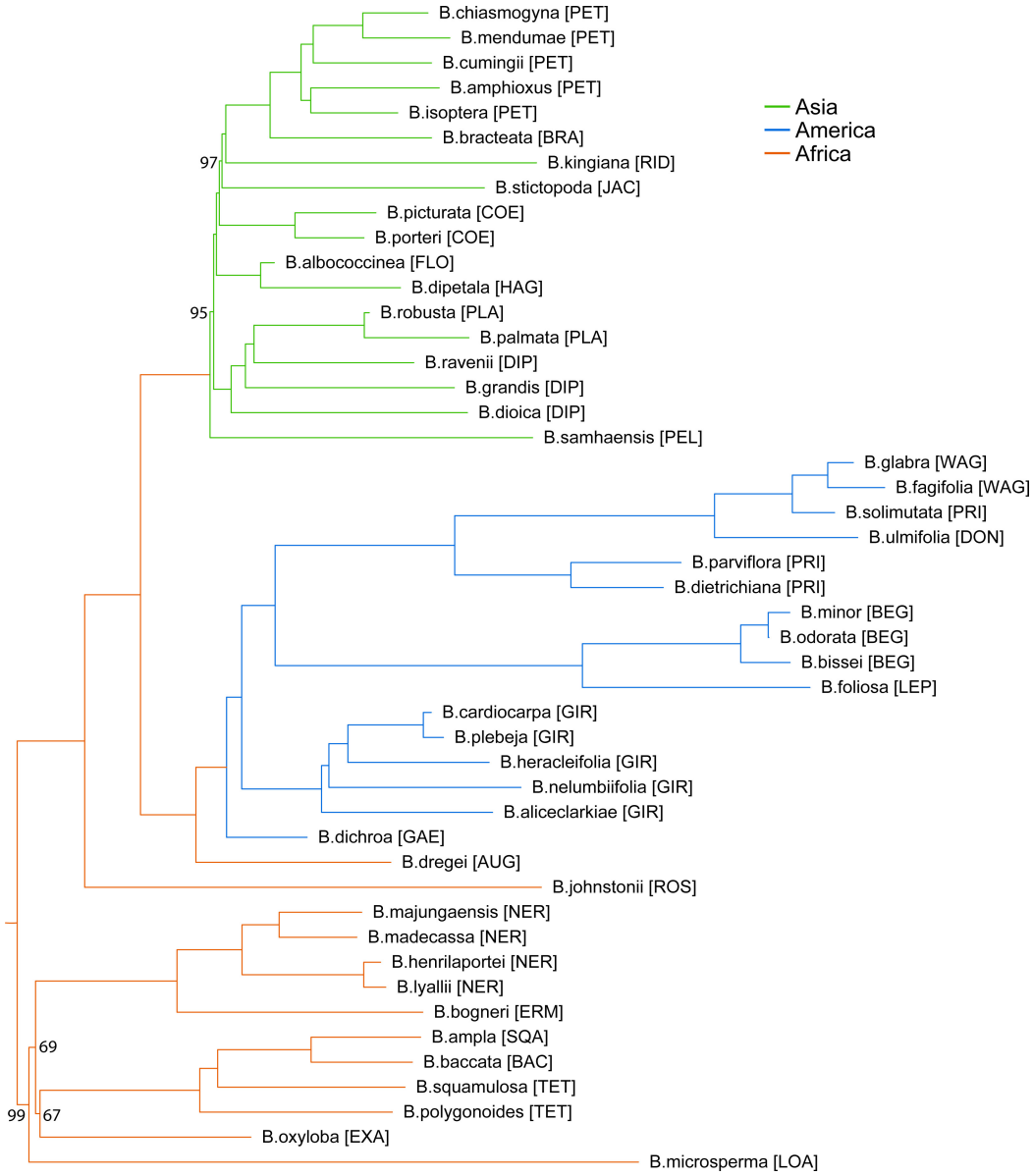

Figure 2. Maximum likelihood phylogeny of *Begonia* based on a concatenated alignment of 1235 nuclear genes. Nodes have 100% fast bootstrap support, unless indicated. Section name abbreviations: AUG, *Augustia*; BAC, *Baccabegonia*; BEG, *Begonia*; BRA, *Bracteibegonia*; COE, *Coelocentrum*; DIP, *Diploclinium*; DON, *Donaldia*; ERM, *Erminea*; EXA, *Exalabegonia*; FLO, *Flocciferae*; GIR, *Gireoudia*; HAG, *Haagea*; LEP, *Lepsia*; LOA, *Loasibegonia*; NER, *Nerviplacentaria*; PET, *Petermannia*; PRI, *Pritzelia*; RID, *Ridleyella*; ROS, *Rostrobegonia*; SQA, *Squamibegonia*; TET, *Tetraphila*; WAG, *Wagenaria*.

for the usually maternal inheritance of both chloroplast and mitochondria. The chloroplast haplotype for the species is near identical to a species that grows in the same part of Palawan, *Begonia quinquealata* C.I Peng, Rubite & C.W.Lin (Hughes *et al.*, 2018a), and it seems likely it has captured both organelles from that species. However, nuclear ribosomal ITS sequence data place *Begonia palawanensis* in a clade of Bornean and Philippine *Begonia* sect. *Petermannia* (Girmansyah *et al.*, 2019), the species of which have a similar caulescent morphology, and hence this placement is the most likely species tree. However, the supported incongruence between the chloroplast and mitochondrial lineages across the genus (see **Figure 1**) means that the universal maternal inheritance for both organelles we observed in the greenhouse experiments either breaks down in some circumstances or is not the normal mode in some species. Although our greenhouse results support a maternal mode of inheritance of chloroplast and mitochondria, we looked at only two interspecies pollination events, and further studies with increased sampling of a diverse range of species are needed to fully understand organelle inheritance in *Begonia*.

The majority (c.80%) of angiosperm genera have strictly maternal inheritance of chloroplasts, with the remainder having biparental or paternal inheritance (Birky, 2008). Although mitochondrial inheritance is near universally maternal in angiosperms (Birky, 2008), it is paternal in at least some members of the Cucurbitales (*Cucumis* L.; Calderon *et al.*, 2012). Given the higher congruence between the nuclear and mitochondrial phylogenies in this study, it seems reasonable to assume that chloroplast capture by a foreign nuclear and mitochondrial background is driving the incongruence between the phylogenies. This could entail the chloroplast coming from the ovule parent, the mitochondrion from the pollen parent or biparental followed by assorting, and the nuclear genome being biparental, with more complete replacement of the foreign nuclear genome through repeated backcrossing. The incongruence could also result from the chloroplast coming from the pollen parent, or at least in part followed by assorting, resulting in the organelle incongruence, with full nuclear genome incongruence again acquired through repeated backcrossing.

Which scenario is the more probable cause of chloroplast capture in *Begonia* is not easy to determine, but a partially selfing breeding system may make capture more likely (Tsitrone *et al.*, 2003). Partial selfing has been demonstrated in wild *Begonia* using molecular data (Hughes & Hollingsworth, 2008; Twyford *et al.*, 2014), and most species in cultivation are self-compatible (Ginori *et al.*, 2022); however, some species of yellow-flowered Africa *Begonia* have been shown to be self-incompatible in greenhouse experiments (Sosef, 1994). Population genetic models show that chloroplast capture occurs faster in populations that have inbreeding depression and also when the selfing rate drops after hybridisation (Tsitrone *et al.*, 2003), which seems plausible in *Begonia* because they exist in small, isolated populations and hybrids often have reduced pollen fertility, leading to reduced male fitness and the ability to self-pollinate. It may be that a few abnormal events of organelle capture have left a disproportionate amount of phylogenetic evidence.

The concatenated nuclear gene phylogeny constructed in this study no doubt hides some complexity, given the propensity of *Begonia* to hybridise. Further work is needed to look for evidence of hybridisation in the nuclear genome at all levels in the *Begonia* phylogeny, from ancient events to recent ones such as the case of *B. palawanensis*. Also, further work is needed on the complexities and evolution of the *Begonia* mitogenome, which has been shown to undergo recombination after hybridisation in plants (Boeshore *et al.*, 1983) and may therefore track more than one phylogenetic history.

Incongruence: biogeographical implications

Biogeographical studies that use phylogenetic evidence are usually based on the assumption that the phylogeny represents the species tree. Such studies on *Begonia* have used nuclear ribosomal ITS data, either alone (Rajbhandary *et al.*, 2011) or in combination with a single chloroplast region (Plana *et al.*, 2004; de Wilde *et al.*, 2011; Chung *et al.*, 2014). Only Chung *et al.* (2014) detected incongruence between the two genomes, but they noted that the combined evidence phylogeny was congruent with the ITS tree. The amount of variable sites in the ITS region means that these studies are overwhelmingly based on tree topologies derived from that locus. Other studies that have focused on ancestral area reconstruction at either regional (Hughes *et al.*, 2015) or continental scales (Thomas *et al.*, 2012; Moonlight *et al.*, 2015) are based entirely on chloroplast data. Given the amount of phylogenetic incongruence between the three genomes (**Figure 3**), clearly neither the ITS region nor the chloroplast genome is likely to represent the species tree, and it is not even certain that a species tree exists for *Begonia* as a whole.

Particularly concerning is the high prevalence of chloroplast capture observed in *Begonia*, especially between geographically close species (Hughes *et al.*, 2018a), because this could bias phylogenies reconstructed from chloroplast genes towards geographical monophyly, which has been noted as a key characteristic of the genus (Hughes & Hollingsworth, 2008). This would lead to an underestimation of dispersal at the species level in studies reconstructing ancestral areas. Conversely, however, at a deep timescale it is only the chloroplast phylogeny that has evidence for two dispersals from Africa to the Americas, evidence for which has not yet been detected using mitochondrial and nuclear data. Future biogeographical studies should be explicit about potential phylogenetic bias and ideally use more than one genome to illustrate conflicting histories.

Incongruence: taxonomic implications

The large *Begonia* sect. *Petermannia* has previously been highlighted as polyphyletic in terms of chloroplast phylogeny (Thomas *et al.*, 2011), having species representing *Begonia* sect. *Baryandra* (as *Begonia* sect. *Diploclinium* in Thomas *et al.*, 2011), *Begonia* sect. *Jackia* (as *Begonia* sect. *Reichenheimia* (Klotzsch) A.DC.), *Begonia* sect. *Bracteibegonia* A.DC. and

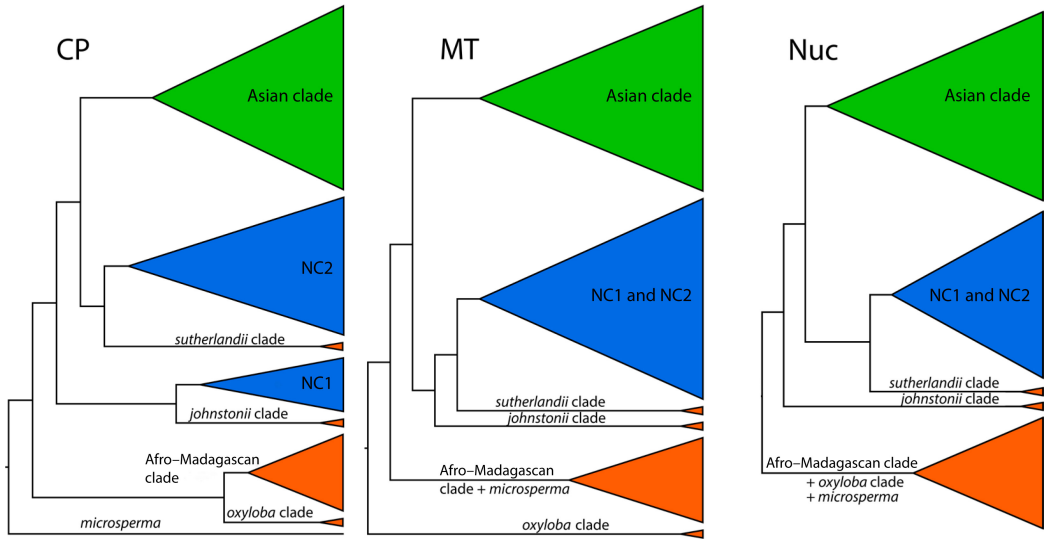

Figure 3. Differences in basal topology of *Begonia* phylogeny shown on diagrammatic representations of maximum likelihood analysis of chloroplast (CP) data (left), mitochondrial (MT) data (middle) and nuclear (Nuc) data (right). Cladograms show topology only, branch lengths are not to scale. NC1, Neotropical clade 1; NC2, Neotropical clade 2.

Begonia sect. *Symbegonia* (Warb.) L.L.Forrest & Hollingsw. nested within it; the results of the present study also show *B. amphioxus*, *B. dimorpha* and *B. malachosticta* (clade PET1 in Thomas *et al.*, 2011; the 'amphioxus clade' in Moonlight *et al.*, 2018) as separate from the rest of *Begonia* sect. *Petermannia* (see **Figure 1**). This is contradicted by mitochondrial phylogenetic relationships (Goodall-Copestake *et al.*, 2010; see **Figure 1**), and also the nuclear phylogeny (**Figure 2**), which shows a monophyletic *Begonia* sect. *Petermannia*. This confirms the hypothesis of Thomas *et al.* (2011) that the polyphyly of the section in the chloroplast phylogeny is the result of chloroplast capture and does not support the merging by Shui *et al.* (2019) of all the sections mentioned above into *Begonia* sect. *Petermannia*.

The mitochondrial and nuclear trees in this study (see Figures **1**, **2**) show *Begonia* sect. *Bracteibegonia* (represented by *B. bracteata* Jack) as sister to *Begonia* sect. *Petermannia*. Further taxon and genome sampling is needed to understand the relationships of *Begonia* sect. *Bracteibegonia*, *Begonia* sect. *Petermania* and *Begonia* sect. *Symbegonia* more fully before any of them can be recircumscribed. Although *Begonia* sect. *Petermannia* is the largest section in the genus, currently having 464 species, it is a diagnosable taxon as delimited by Moonlight *et al.* (2018), defined by morphological and anatomical characters including a caulescent habit and absence of rhizomes or tubers, inflorescence morphology (protogynous inflorescences), and potentially also anther anatomy (Thomas *et al.*, 2011).

Species identification within *Begonia* sect. *Petermannia* is currently aided by geographical rather than taxonomic or morphological subdivision. Geography-based subdivision allows the delimitation of smaller groups of names, due to the near 100% island endemism across the Malay Archipelago, where the bulk of species are found. Although a revision of the section is lacking, the photographs in *A Guide to Begonias of Borneo* by Kiew *et al.* (2015) show how character-rich the section is in terms of habit, indumentum, inflorescence structure, androecium form and stigma shape (the latter two characters are generally poorly known and described for most *Begonia*, but they are a vastly underused source of taxonomic information). Further exploration by those with a good knowledge of the section is needed to provide information on which to base decisions on the utility and feasibility of recircumscribing it.

The topology of the African clades in all three phylogenies is congruent with the classifications of both Moonlight *et al.* (2018) and Shui *et al.* (2019), except for the paraphyly of *Begonia* sect. *Tetraphila* A.DC. in the nuclear phylogeny (represented by *B. polygonoides* Hook.f. and *B. squamulosa* Hook.f) with respect to *Begonia* sect. *Baccabegonia* J.M.Reitsma and *Begonia* sect. *Squamibegonia* Warb.

The phylogenetic incongruence in Neotropical *Begonia* is largely between rather than within sections, based on the current sampling, but given the amount of incongruence, it is likely that this will not hold with further investigation. *Begonia* sect. *Gaerdtia* (Klotzsch) A.DC., represented by *B. macduffieana*, is highly incongruent between the organelle phylogenies, and therefore the other 17 unsampled species in the section need further investigation.

Current state of Begonia *taxonomy and future needs*

Taxonomic revisions have been published for some smaller sections of *Begonia* (*Begonia* sect. *Mezierea* (Gaudich.) Warb., Klazenga *et al*., 1994; *Begonia* sect. *Loasibegonia* A.DC. and *Begonia* sect. *Scutobegonia* Warb., Sosef, 1994; *Begonia* sect. *Peltaugustia*, Hughes & Miller, 2002; *Begonia* sect. *Pilderia* (Klotzsch) A.DC., Moonlight & Jara-Muñoz, 2017; *Begonia* sect. *Symbegonia*, Gagul *et al.*, 2018; and *Begonia* sect. *Australes* L.B.Sm. & B.G.Schub., Tebbitt, 2020), and for combinations of section and geographical area (*Begonia* sect. *Petermannia* and *Begonia* sect. *Diploclinium* on Palawan, Hughes & Coyle, 2009, Hughes *et al.*, 2010; *Begonia* sect. *Petermannia* and *Begonia* sect. *Sphenanthera* (Hassk.) Warb. [now a synonym of *Begonia* sect. *Platycentrum* (Klotzsch) A.DC.] on Sumatra, Hughes & Girmansyah, 2011, Girmansyah *et al.*, 2019).

Africa has fairly comprehensive coverage in revisionary and floristic works, due to the amenable size of its flora but also because its *Begonia* flora benefitted over a period of several years from the taxonomic work conducted by a collaborative group of *Begonia* specialists (de Wilde, 1985), resulting in several monographic treatments (de Wilde &

Arends, 1980; de Wilde, 2002; Klazenga *et al.*, 1994; Sosef, 1994). Modern floras are available for southern Africa (Hilliard, 1976), South–Central Africa (Kupicha, 1978), Madagascar (Keraudren-Aymonin, 1983) and Tropical East Africa (Plana *et al.*, 2006).

In Asia, modern floristic works are available for Bhutan (Grierson, 1991), China (Gu *et al.*, 2007), Thailand (Phutthai *et al.*, 2019), the Solomon Islands (Lin *et al.*, 2021a) and Sri Lanka (Jayasuriya, 1983), alongside older treatments for India and the Philippines (Clarke, 1879; Warburg, 1904) and continental Southeast Asia (Gagnepain, 1921). Modern regional floras have been published for Peninsular Malaysia (Kiew, 2005), northern Sulawesi (Ardi & Thomas, 2022), southeastern and Southwest Sulawesi (Ardi *et al.*, 2018; Thomas & Ardi, 2020) and Northeast India (Camfield & Hughes, 2018), with some works available for smaller areas such as the Melinau Limestone in Gunung Mulu National Park (Julia *et al.*, 2013), the Matarombeo karst in Sulawesi (Thomas *et al.*, 2018) and Bidoup-Nui Ba National Park in Vietnam (Lin *et al.*, 2021b).

Floristic coverage in relatively modern works is better for the Americas but of variable completeness. The most up-to-date works include those for Argentina (Delfini, 2017), Cuba (Calzado, 2000), the Dominican Republic (Burt-Utley, 1991), Ecuador (Smith & Wasshausen, 1986), Mesoamerica (Burt-Utley, 2015) and Brazil (in progress) (Jacques & Gregório, 2020). Additionally, there are further regional works available for Brazil, for example Bahia (de Souza Gregório *et al.*, 2016), Serra do Brigadeiro State Park (Delfini & Souza, 2016), Ceará (Lima *et al.*, 2020), Macaé de Cima Ecological Reserve (Jacques, 1996) and Serra dos Carajás (Kollmann, 2016); for Mexico (Nova Galiciana; Burt-Utley & McVaugh, 2001); and for Venezuela (Venezuelan Guyana; Steyermark, 1997). Recently, some illustrated popular guidebooks have been published, covering Arunachal, India (Morris, 2017), China (Shui & Chen, 2017), Borneo (Kiew *et al*., 2015) and Asia (Hughes *et al.*, 2018b), which have a broad appeal but also are useful in aiding identification, particularly when images are included of the type or from the type locality.

For the most diverse tropical areas, however, particularly within Southeast Asia, revisionary taxonomy of any scale is out of the question because of the ongoing species discovery phase, which would very quickly render any work obsolete. Future taxonomic work will have to deal with two types of issue: first, large groups with many similar species, leading to difficulties of species delimitation and identification; and second, areas with great morphological diversity and many phenetic gaps, such as Vietnam, where some species defy classification due to having unique sets of characters not found in any existing section. DNA evidence, obtained by either phylogenetic or barcoding, will be invaluable in resolving both these issues.

Although high-throughput sequencing continues to become more affordable, Sanger-based barcodes are currently more widely accessible in terms of laboratory and analytical logistics. The nuclear genes in our bait set have quite low levels of variation between species, and we do not consider them useful for barcoding at present. Given the large

amounts of data available for the three chloroplast regions *ndh*A intron, *ndh*F–*rpl*32 spacer, and *rpl*32–*trn*L spacer, and for nuclear ribosomal ITS, a combination of these will provide a functional barcode to aid species identification and guide sectional placement. All these regions are easily amplified and sequenced using Sanger technology, or they can be assembled using high-throughout sequencing from either genome skims or bait capture data.

A workable sectional treatment is needed to enable new species to be classified, to facilitate species identification and future revisionary work, and to ensure that such works have long-term relevance and utility. Future floristic work will also build on regional revisions and therefore also benefit from a stable and useful sectional classification. A valuable next step is to populate the forthcoming World Flora Online (WFO, 2022) Begoniaceae account with descriptions and images as a resource for identification and for supporting regional floras and revisions. This will need a collaborative approach.

A manifesto for Begonia *taxonomy*

We wish to set out two sets of guiding principles for *Begonia* taxonomy, the first dealing with the operational aspects of creating and disseminating classifications of *Begonia*, and the second dealing with technical and systematic guidelines. The Legume Phylogeny Working Group provides an inspiring example of collaboration, and we have arrived at a similar set of general guiding principles, including the use of both Linnean and rank-free clade names (Borges *et al.*, 2013; Bruneau *et al.*, 2013).

The operational principles are that future *Begonia* classifications should be:

- electronically available and open access
- created by an inclusive collaboration
- peer reviewed.

The systematic principles are that:

- *Begonia* should be treated as a single genus
- phylogenetic incongruence should be considered
- a combination of molecular phylogenetic and morphological information should be used
- utility should be the primary function of any new classification
- Linnean sections should be retained and circumscribed to be monophyletic
- clade names can be used informally above and below the section.

Operational principles

To be accessible to the broader community, a classification needs to be electronically available and open access, such as the classifications of Doorenbos *et al.* (1998) and

Moonlight *et al.* (2018), the latter being available from the Begonia Resource Centre (Hughes *et al.*, 2015–). There is also a need to make other taxonomic information, in addition to classifications, also freely available; such information includes protologues, images of types and other specimens, and distribution maps. These are currently dispersed throughout the scientific literature, but much has been made available via the Sulawesi Begonia Data Portal (Thomas *et al.*, 2013) and the Begonia Resource Centre (Hughes *et al.*, 2015–). *Begonia* classifications available only as hard copy quickly become out of date due to the high rate of publication of taxonomic research on the genus.

The development of any classification should be collaborative, and whenever possible, should be led by or involve experts from the region where the classification will be used. We hope that the formation of the Begonia Phylogeny Group will foster this approach, which will not only make use of regional expertise and experience but will also encourage adoption of the classification and hence future taxonomic stability. In addition to a broad collaboration, peer review will reduce errors and poor taxonomy.

Systematic principles

Begonia should be treated as a single genus

The last genus to be sunk into *Begonia* was *Symbegonia* Warb. (Forrest & Hollingsworth, 2003), placing every species in the family in *Begonia* apart from *Hillebrandia sandwicensis*. The rank of section has served taxonomic endeavours well and allows movement of species between sections without the upheaval of new combinations. This is all the more important due to the high amount of taxonomic activity in *Begonia* at present.

Phylogenetic incongruence should be considered

The phylogenetic incongruence confirmed in the present study should be taken into account in new classifications. For the immediate future, chloroplast sequence data will probably continue to provide a source of insight into phylogenetic relationships. In terms of species number, the highest amount of data is available for chloroplast sequences, and the addition of new taxa is relatively simple.

In combination with morphology and the insights provided by the existing nuclear and mitochondrial phylogenies, an understanding of the most likely species tree is developing. However, a goal should be to increase the sampling of nuclear DNA sequence data, and the species sequenced here using the Hyb-Seq bait set developed by Michel *et al.* (2022) provide a foundation on which to build. Even very old herbarium specimens of *Begonia* have the potential to yield large amounts of useful sequence for the nuclear and organelle genomes (Forrest *et al.*, 2019). Future sampling could capitalise on this and should focus on type species, type specimens, species complexes, and taxa in parts of the phylogeny in which there is already known to be high incongruence between chloroplast and mitochondrial gene trees.

A combination of molecular phylogenetic and morphological information should be used
The use of molecular phylogenetic data has revolutionised our knowledge of *Begonia* evolution, but as a basis for a useful classification that aids species identification, it is of little use unless considered in the light of species morphology. To maximise identification utility, classifications should ideally focus on delimiting groups that are diagnosable morphologically, as well as supported phylogenetically. It is unlikely that single synapomorphies for each section will be found, given the high degree of homoplasy documented in the genus (Forrest *et al.*, 2005; Thomas *et al.*, 2011), but character combinations have the potential to be diagnostic.

Vegetative characters, and some floral characters, such as stigma form and anther and androecium morphology, have not been used to their full potential in infrageneric *Begonia* classification and especially need further investigation. However, detailed documentation of morphological, anatomical and chromosomal characters already known to be taxonomically useful within *Begonia* is also required and should ideally be produced on a collaborative basis to maximise coverage within the genus. The few existing studies, such as those on leaf micromorphology (Cuerrier *et al.*, 1991a, 1991b) and seed micromorphology (Bouman & de Lange, 1983; de Lange & Bouman, 1992, 1999), continue to be sources of useful information when constructing infrageneric classifications.

Utility should be the primary function of any new classification
Although sectional monophyly is an ideal to aim for in *Begonia* classification, monophyly at all costs is unlikely to provide a useful taxonomy. A workable sectional treatment is needed by the taxonomic and conservation community to enable the flood of new species to be classified, to facilitate species identification and future revisionary work, and to ensure that such works have long-term relevance. As we have set out in this paper, a good classification should be useful for delimiting natural (monophyletic) groups and facilitating identification of species. Therefore, we recommend avoiding large sections with many hundreds of species and large amounts of morphological variation. Monotypic sections also often lack utility and are to be avoided whenever larger diagnosable groupings can be made.

Linnean sections should be retained and circumscribed to be monophyletic
We consider a combination of Linnean sections and informal clade names as the best approach while we are in the middle of a discovery phase in terms of phylogeny and species diversity. We consider a proliferation of Linnean ranks such as subgenus, series, supersection and subsection to be of little use, and it can lead to a proliferation of names for their own sake; it is also prone to create instability as we gather more data. We discussed the potential of using the PhyloCode in *Begonia*, potentially as a way to indirectly refer to paraphyletic groups using clade names (e.g. species in clade X, but not in clade Y nested within it). However, given the problems of phylogenetic incongruence and uncertainty in the genus, we felt that it does not offer a stable solution at the present time.

Clade names can be used informally above and below the section
Informal names have been used successfully in *Begonia* below the rank of section (e.g. the '*tiliifolia*' group (Tebbitt *et al.*, 2017) and the '*calcarea*' group (Kiew *et al.*, 2016) and for larger groups above section (e.g. the *Diploclinium* grade, the *Wagenaria* clade and Malagasy *Begonia* (MB) (Moonlight *et al.*, 2018). These are flexible, come without nomenclatural restrictions of sections, and are useful while so much taxonomic work is in progress. However, the naming of informal groups should still be carefully considered under the same criteria of phylogeny, morphology and utility.

Conclusion

There has been a resurgence of activity in *Begonia* taxonomy in the past 20 years, which has gathered pace as baseline knowledge has expanded and facilitated further work and encouraged new taxonomists to join the endeavour to document species diversity in the genus. Considerable taxonomic resources are now available for areas that were previously *terra incognita*, such as Borneo and Sulawesi. When the discovery phase begins to slow in such regions, it will be time to move into a revisionary phase, with the most tractable place to start being regional monographs on sections of the genus (Atkins *et al.*, 2021) before moving on to larger Flora accounts. Such work needs a stable and useful classification to support it, and we hope we have laid the foundation of that in this paper. We welcome new researchers who wish to join the group for collaboration and support.

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Author contributions and recommended citation

M.H. drafted the manuscript following a group discussion and with extensive comments from P.W.M. and W.P.G.-C.; M.H. produced the figures; M.S., Y.-H.T., L.C.-D. and C.K. carried out the bioinformatics work; D.F., E.D., W.P.G.-C., Y.-H.T., K.-F.C., H.P.W., P.W.M., M.S., M.H., L.C.-D., R.L., L.D.K.M. and D.C.T. provided data; M.H. and M.S. did the phylogenetic analyses; and all authors reviewed the manuscript. The authors are listed alphabetically, and the recommended citation for this paper is: Begonia Phylogeny Group (2022). Resolving phylogenetic and taxonomic conflict in *Begonia*. Edinburgh Journal of Botany 79, *Begonia* special issue, Article 1928: 1–28. https://doi.org/10.24823/EJB.2022.1928.

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Supplementary material

Supplementary material for this article is available from the *Edinburgh Journal of Botany* online portal.

Supplementary file 1. Chloroplast and mitochondrial phylogenetics: accessions from which the sequences were obtained.
Supplementary file 2. Chloroplast alignment data.
Supplementary file 3. Chloroplast partition data.
Supplementary file 4. Mitochondrial alignment data.
Supplementary file 5. Mitochondrial partition data.
Supplementary file 6. Chloroplast likelihood phylogeny.
Supplementary file 7. Mitochondrial likelihood phylogeny.
Supplementary file 8. Chloroplast nexus file.
Supplementary file 9. Chloroplast Bayesian phylogeny.
Supplementary file 10. Mitochondrial nexus file.
Supplementary file 11. Mitochondrial Bayesian phylogeny.
Supplementary file 12. Nuclear phylogenetics: accessions from which the sequences were obtained.
Supplementary file 13. Nuclear alignment data.
Supplementary file 14. Nuclear likelihood phylogeny.

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